Group structure and reproductive behaviour of Siamese fireback *Lophura diardi* and silver pheasant *L. nycthemera* at Khao Yai National Park, Thailand

TOMMASO SAVINI[*] and NITI SUKUMAL
Conservation Ecology Program, King Mongkut's University of Technology Thonburi, Conservation Ecology Program, School of Bioresources & Technology, 83 Moo 8 Thakham, Bangkhuntien, Bangkok 10150, Thailand.
[*]Correspondence author - tommaso.sav@kmutt.ac.th; tommasosavini@gmail.com

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Abstract Over the past 25 years, a range change has been observed in the Siamese fireback in Khao Yai National Park, Thailand. It has moved from lower to higher altitudes and is now found in areas where previously only silver pheasant were reported. To investigate this new phenomenon, thought to have been triggered by a change in the general forest structure within the region, a long-term project was initiated. This paper investigates the breeding behaviour of these two species to establish if similarities exist, which in an extreme case could result in inter-breeding. The data collected are based on colour-ringed (n = 7) and radio-tagged individuals (n = 2), observed at fifteen minutes intervals in order to examine social interactions between individual males and females and between males themselves. Preliminary analyses undertaken after one breeding season (2007), indicates differences between the two species' mating strategies. Siamese fireback show a strong skew, with a dominant male largely monopolizing proximity, and therefore access to all the females in a group, while silver pheasant were observed to have a lower skew, with all males in a group sharing almost equal proximity to females. In addition, Siamese fireback males were also sporadically observed joining silver pheasant groups. With the data so far available, some cross-species breeding appears possible as the mating systems of both species do appear to stimulate the formation of mixed-species groups during the breeding season.

Keywords Inter-species hybridization, mating strategies, mixed-species groups, species syntopy, Thailand

Introduction

Observations conducted in Khao Yai National Park, central Thailand, during the past twenty-five years have reported a range change for Siamese fireback *Lophura diadri*, now found at higher elevations, around 800 m, where previously silver pheasant *Lophura nycthemera* was mostly observed (Round & Gale, 2008). The suggested explanation for this expansion is climatic change, which during the past 100 years has affected habitat change on a global scale, by increasing average temperatures by about 0.6 C (Houghton *et al.,* 2001). One consequence of rising temperatures is the change in evapotranspiration, which is higher in the lowlands than in montane and sub-montane areas. This change in habitat characteristics has been suggested by Round & Gale (2008) as the primary cause leading to the recent significant increase in the numbers of Siamese fireback relative to the "resident" population of silver pheasant in the study site. Expansion along an altitudinal axes for lowland species, (both plants and animals), appears to be a general pattern and perhaps a consequence of microhabitat changes (Karr & Freedmark, 1983) due to rising temperatures (increasing evapotranspiration).

In one of the few studies conducted on avifauna in the tropics, specifically in the cloud forest of Costa Rica, Pounds *et al*. (1999) observed rapid changes in species composition. Here the colonization of montane habitat by non-montane species was a result of the mist frequency decline creating drier habitat.

Although on a broad scale species of the genus *Lophura* may appear sympatric in few occasions, they are typically ecologically separated by topographical barriers, as in Sumatra were *L. ignita* is a marked lowland species replaced at higher elevations by *L. hoogerwerfi*, in the north of the island, or *L. inornata*, in the southern part (BirdLife

International 2001), or habitat differences, as in West Malaysia where *L. ignita* inhabit wet riverine forest while *L. erythrophthalma* prefer drier slopes (Davison, 1981). Silver pheasant and Siamese fireback appear sympatric in their wide range, but ecologically segregated. In Laos they are naturally segregated by different elevations with silver pheasant usually predominates at 500 m or above while Siamese fireback is found in the lowlands (Thewlis *et al*., 1998). A similar segregation pattern has been so far observed in Thailand (Lekagul & Round, 1991), with the exception of Khao Yai National park (Round & Gale, 2008).

In Vietnam, where the encounters between two *Lophura* species has sporadically occurred, hybridization was observed, resulting in the former *L. imperialis* (Hennache, *et al.,* 2003) once considered a critically endangered species (McGowan & Garson, 1995).

In this work we present the preliminary results of an ongoing study focusing on the effects of a recently observed “forced” sympatry between the two congeneric species, Siamese fireback and silver pheasant in Khao Yai National Park. Our goal is to evaluate the possibility of hybridization between these two species now living in “forced” syntopy. In order to define the risk of hybridization between the two species, we first hypothesize there is an overlap in their mating period and then strong similarities in their mating strategies and in the social composition during their mating periods.

Methods

Study Site

The study was started in January 2007 at the Mo Singto Long Term Biodiversity Research Plot, Khao Yai National Park, Thailand (2,168 km^2; 101°22′ E, 14°26′ N), in slightly hilly terrain, 730 - 890 m above sea level (for details regarding the plot see Brockelman *et al.,* 2002). Khao Yai is largely a seasonally wet, evergreen forest (Kerby *et al.,* 2000; Kitamura *et al.,* 2004). Based on data from 2000 to 2004 it experiences a distinct dry season (November – April) and wet season (May – October) with an average precipitation of 2697 mm (range 2976 to 2297 mm) (Savini *et al.,* in press a). Average daily temperature varied annually between 18.7° C and to 28.3° C, and mean humidity ranged from 64.6% during the dry season to 77.1% during the wet season (Savini, *et al., in press(a)*).

Study species

Both pheasant species found in syntopy in Khao Yai National Park, silver pheasant (SPH) and Siamese fireback (SMF) are found sympatrically over much of their southeastern range (Dickinson, 2003). In their range in Thailand these two species are largely segregated by elevation and, consequently, it can be assumed by habitat moisture. Silver pheasant have a montane and submontane distribution, with elevations of 700 m and above, while Siamese fireback is characteristically a lowland species, inhabiting forest in plains and foothills to a maximum elevation of 700 m (Lekagul & Round, 1991; Robson, 2000).

Animal capture and marking

From January 2006 onwards pheasants were caught using mist-nets and snare traps made from bamboo and soft polyester string. Mist nets were set on the ground to a height of approximately 3 m. We used a net of 12 m, 3 shelves, 2.75 m high with mesh of 150 mm. All pheasants caught were ringed with Thai Royal Forest Department (RFD) (now Department of National Park, Wildlife and Plant Conservation) metal rings (11A size), and colour-banded with a two-colour combinations on the left leg and one colour-ring and a metal ring on the right leg, so as to facilitate individual identification in the field. Each bird was weighed, measured and examined for stage of moult.

From May 2007 birds were fitted with 15-gram, radio transmitters, model RI-2B with a life span of 24 months and made by Holohil Systems Ltd. The RI-2B is designed as a necklace mounted transmitter. The transmitter rests on the bird’s breast while the antenna loops around the neck and emerges behind the head. The collar is made of flexible elastic attached to the transmitter at two points.

Group composition

Data on pheasant group composition were collected both *at libitum* by all researchers working on the botanical plot as well as by the authors when conducting specific searches for pheasants. Once a group was detected, data on species and sex composition, time of observation, group location and presence of marked birds were recorded.

Mating behaviour

When marked birds were present in a group, 15-minute focal sampling (Altman, 1974) was used to record mating behaviour. We recorded data on proximity between males and females. In this regard we considered the focal male as the centre of a circle and we continuously recorded the position of females, and other males, in hypothetical circles of 0.5, 1, 2, 5, 10 and 20 m radius respectively. Proximity was here used as a *proxy* for male access to females as copulation is rarely observed in the wild due to their short duration.

Statistical analysis

Due to relatively small sample size data were analysed with non parametric tests such as Mann-Whitney U tests and Wilcoxon test to compare differences in group sizes and proximities between individuals using SPSS (version 13.0) and R (version 2.8.1) software.

Results

Group composition and dynamics

During the entire mating season (January to May) group size was generally similar between the two species (Mann-Whitney U, Z = -0.742, n = 10, P = 0.548) as was the sex ratio (Mann-Whitney U, Z = -0.841, n = 10, P = 0.421) suggesting no significant difference in social structure (TABLE 1). During just the months of January and February, when peak mating activity was recorded for both species, a relatively high number of solitary SMF males were observed (average 44% of social units, n = 23, s.e. = 6). These male units were primarily composed of one male (rarely 2 males). For SPH the average proportion of solitary males was much lower (average 17%, n = 12, SE = ±3).

Mating behaviour and group cohesion

Proximity to females between males of the same group differed between the two species (FIG. 1). For SMF there was a significant difference between proximity of males and females (Wilcoxon test, W = 214, n = 28, P = 0.0019), where one male was always in closer proximity to females, relative to the other males present, but not for SPH (Wilcoxon test, W = 314.5, n = 24, P = 0.4664).

Mixed-species groups

Two mixed-species groups were observed on four occasions during the study period. In all events they consisted of a SPH stable social unit with a male SMF attending it. In detail: Group A (1 male and 2 female SPH plus 1 male SMF) was observed three times. On one occasion the Siamese fireback male participated in vocal interactions with the rest of the group. Group B (1 male 2 females and 7 chicks of silver and 1 male fireback) was observed once, and on this occasion the two males were fighting.

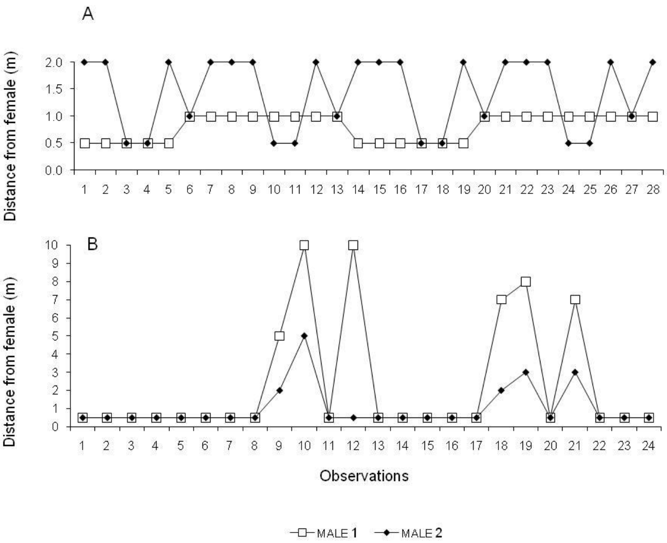

FIG. 1 Variation in distance between males and females within each social unit between Siamese fireback (A) and silver pheasant (B).

Discussion

Our results show overall similarities between the number of individuals in a social unit as well as the sex ratio between two pheasant species. However, the percentage of social units composed of floaters, solitary animals excluded by stable groups, or in a few cases by a pair of floaters, during the peak of the mating season varied between the two species, with Siamese fireback showing a much higher proportion than silver pheasant (TABLE 1). From the point of view of access to females, measured as proximity between males and females, there appears to be a difference between the two species. In SMF, the proximity to females by the two males present in a single social unit was significantly different meaning that one male was consistently closer to the females and might have greater access to them. In SPH no significant difference was found in the proximity of different males to the females within the same social unit suggesting that in this case, both males have similar potential access to females.

From a cost-benefit point of view, we can expect a multi-male multi-female social unit to be stabile if, and only if, the minimum value in copulation share requested by a subordinate male, defined as "*Pmin*", is equal or less than the maximum share granted by the dominant male, defined as "*Pmax*", (Johnstone, 2000). A social unit will be defined as having a "high skew" when the dominant male monopolizes most of the copulations, while, a "low skew" will be the result of a large share in copulations between the different males in the unit. The factors defining the copulation share may vary between dominant and subordinate males as "*Pmax*" will be related to the extent a dominant male needs the presence of subordinate males, while "*Pmin*" will depend on the need of subordinates to remain in the social unit. In cases where the subordinate males receives less than a minimum share in reproduction, it will be best for them to depart the group and try to breed elsewhere. On the other hand, if the dominant male has to concede a higher share than is expected it will be best for him to evict the subordinates (Vehrencamp, 1983; Johnstone & Cant, 1999; Johnstone, 2000).

TABLE 1 Group composition for *L. nycthemera* and *L. diardi* at the Mo Singhto Long Term Biodiversity Plot (Khao Yai National Park, Thailand).

Species	Month	Group size (average)	Sex ratio (male/female)	Group (observed)	Floater (observed)
L. nycthemera	Jan	4.1	1/1.3	6	1
	Feb	3.9	1/1.3	4	1
	Mar	3.6	1/1.2	2	4
	Apr	3	1/0.8	1	7
	May	3.5	1/0.7	0	2
L. diardi	Jan	4	1/0.8	8	5
	Feb	4	1/1.6	9	5
	Mar	3	1/1	10	1
	Apr	3	1/0.5	15	5
	May	0	0	6	9

Several factors have been suggested as defining the amount of copulation share. (1) The origin of each adult male within the social unit: parental relationships have been explained as one mediating factor in the sharing of copulations as shown in African lions *Panthera leo* (Parker *et* al, 1991) and in white-browed scrub wrens *Sericornis frontalis* (Whittingham *et al.*, 1997) where closely related males show a higher skew in reproduction versus "outsiders", as the gain in inclusive fitness for subordinates (Clutton-Brock, 1998) will maintain them in the social unit. (2) The cooperation in territorial defence is often explained as way extra males might collaborate with the breeding animals in order to remain in the home range (Cockburn, 1998). (3) Simple territorial defence can be combined with overall habitat quality. In low quality habitat, home ranges have to be expanded to meet the needs of reproductive females and extra help in territorial defence is required as shown in the *Porphyrio porphyrio* (Jamieson, 1997).

Currently our preliminary results show the presence of high reproductive skew in Siamese fireback and low reproductive skew in silver pheasant. However, we are not yet able to explain why this difference in mating system occurs. As their home ranges appear too large compared with their daily travel route (Sukumal, unpublished data); the assumption proposed by Mitani & Rodman (1979) for territorial behaviour, for which animals should travel a daily travel route long enough to ensure the encounter of their territory boundary at least once a day, can be rejected for both species. We can exclude then that the factor triggering this reproductive skew is to be found in various levels of help needed by dominant males in maintaining territories (Jamieson, 1997; Cockburn, 1998). Future work will focus on the investigating the risk of dominance take over, together with the cost of a floater status, for which both dominant males and subordinate will need to "cooperate". Furthermore, genetic relationships among animals in the study area are still completely unknown and thus the inclusive fitness hypothesis proposed by Parker *et al.* (1991) cannot currently be tested.

The striking difference we observed in the mating organization between both species might explain the specific presence of mixed-species social units we have observed. Although the number of social units showing both pheasant species are relatively few, with only two units observed over a year study period, they appear to be relatively stable with strong interactions among the individuals, calling and fighting. What appears interesting is the composition of these groups with each time a Siamese fireback male, possibly a floater ejected by a dominant Siamese fireback male, aggregating with a silver pheasant social unit. Aware of the fact that the sample size is small, we however can hypothesize that such a social constellation might be the result of the difference in skew level between the two species. Subordinate Siamese fireback males, who face ejection pressure in their con-specific groups, might migrate to silver pheasant group where such pressure is reduced and will reduce the costs incurred as floaters.

It is still unknown if the two species can cross-breed, as, so far, no hybrids have been observed in the area. However, what we have observed, although based on a limited data set, does not exclude the possibility of such an event taking place as already observed in captivity producing sterile females and fecund males (Ghigi, 1968).

In order to test the possibility of cross-breeding we first hypothesized a strong overlap in their mating period. For both species, peak mating strongly overlap even if a slight variation is observed with Siamese fireback females initiating nests slightly earlier than Silver pheasant. We also hypothesized a strong similarity in their mating strategies and social composition. While social composition is rather similar (TABLE 1), mating strategies differ between the two species but in a way that may stimulate the formation of mixed-species social units in which strong interactions are observed and the risk of cross-breeding cannot be excluded.

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Biographical sketches

TOMMASO SAVINI graduated from Liege University (Belgium) with a dissertation on social variability and reproductive ecology of white-handed gibbons. He is currently a lecturer at King Mongkut's University of Technology Thonburi (Thailand) focusing his research mainly on galliform behavioural ecology but also on other bird groups and primate ecology. NITI SUKUMAL got his bachelor degree on Environmental Science at Khon Khaen University (Thailand). He is currently ending his master dissertation on the habitat use, movement pattern and home range of Siamese fireback and silver pheasant. He is also assisting research on other bird species ecology.